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DOI: https://doi.org/10.1093/beheco/arz112

Drought decreases cooperative sentinel behaviour and affects vocal coordination in meerkats

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Running title: Effect of drought on cooperative sentinel behaviour

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ABSTRACT

Cooperative breeding often evolved in harsh and arid habitats characterised by high levels of environmental uncertainty. Most forms of cooperative behaviour have energetic costs and previous studies have shown that the contributions of individuals to alloparental provisioning are conditional on the food intake of individuals. However, the effect of naturally occurring, extreme environmental conditions on the persistence of costly forms of cooperative behaviours and their coordination by communication remain unknown. Here, we show that in meerkats (*Suricata suricatta*) the probability to act as sentinel, a cooperative vigilance behaviour, was the same for typically occurring dry and wet conditions, but significantly reduced during a drought condition with almost no rain, especially in young individuals, members of small groups and groups with pups. The duration an individual stayed on sentinel guard, however, was most reduced during dry conditions. Besides reductions in sentinel behaviour, the vocal coordination of foraging meerkats differed when comparing drought and wet conditions. Individuals responded more strongly to playbacks of sentinel 'all-clear' calls and close calls, resulting in less vigilance and more foraging behaviour during the drought condition. We conclude that while meerkats are adapted to commonly occurring dry periods with low rainfall, the extreme drought period with almost no rain, led to a decrease of the frequency of costly forms of cooperative behaviours in favour of behaviours that maximize direct fitness benefits and also affect the vocal coordination among group members.

Key words: drought, cooperative breeders, sentinel behaviour, sentinel calls, acoustic communication

INTRODUCTION

Both in birds (Jetz and Rubenstein, 2011) and mammals (Lukas and Clutton-Brock, 2017), cooperative breeding systems, where individuals forego their own independent reproduction

while helping others in the group to rear their young, are commonly associated with environments where resources are scarce. In many of these environments, rainfall and temperature vary widely within and between years (Jetz and Rubenstein, 2011; Lukas and Clutton-Brock, 2017), generating unpredictable fluctuations in resource availability that are commonly associated with variation in breeding success and survival (Clutton-Brock et al., 1999a; Dai, 2011). A recent study on cooperatively breeding birds showed a decrease in cooperative provisioning of young by adult group members during days with unusually high temperatures (Wiley and Ridley, 2016) and previous studies of meerkats (*Suricata suricatta*) have provided experimental evidence that cooperative behaviours are conditional on foraging success and are reduced when daily weight gain of animals is low (Clutton-Brock et al., 2001; Clutton-Brock et al., 1999b). Together, these results suggest that cooperative breeders need to adjust their investment in cooperative behaviours in relation to variation in weather conditions as well as in food availability, especially in response to extreme events, such as droughts, defined as prolonged periods with rainfall significantly below the level received in commonly occurring dry years (Botai et al., 2016). Currently, the effect of naturally occurring, extreme environmental conditions, including reduced food availability, on the persistence of cooperative behaviours has not been explored.

It has been suggested that cooperative breeders may have evolved a more complex communicative system than less social species in order to coordinate group living and cooperative activities (Freeberg et al., 2012; Leighton, 2017; Manser et al., 2014). It is well known that social factors, such as sex, life history stages, or dominance status, influence the behavioural responses to vocal signals (Fischer et al., 2004; Mitani and Brandt, 1994; Snowdon and Elowson, 1999) but the extent to which extreme environmental conditions affect vocal coordination remains unclear. For example, warning or alert calls that are not associated with an immediate threat but rather with a general increase in perceived predation risk or uncertainty might be more likely to be ignored during adverse environmental conditions when individuals need to maximize foraging in order to survive. Thus, drought

conditions might affect the behavioural responses of individuals to specific vocal signals and the coordination of cooperative behaviour.

In this study, we investigated potential differences in cooperative sentinel behaviour and its vocal coordination in meerkats between a year of drought, three years of dry conditions and three years of wet conditions (Table 1). Meerkats forage in small groups from 3 to 50 individuals composed of different age classes (pups < 3 months, juveniles 4-6 months, subadults 7-12 months, yearlings 13-24 months and adults > 24 months) (Clutton-Brock et al., 1999a; Clutton-Brock et al., 2006). Each group consists of a dominant, reproductive pair and subordinates, which help to rear the dominant pair`s offspring by providing them with food and protection (Clutton-Brock et al., 1998). Meerkats have an elaborate sentinel system where one individual is on raised guard at an elevated location, scanning the surroundings for the presence of predators and alerting the group in case of danger (Clutton-Brock et al., 1999b). Besides alarm calls elicited in response to an approaching predator (Manser, 2001; Manser et al., 2001), sentinels also produce functionally specific sentinel calls, which inform the rest of the group about the guard`s temporary perceived predation risk and lead to the adjustment of vigilance behaviours by foraging group members (Manser, 1999; Rauber and Manser, 2017). Sentinel calls include calming calls, which have an 'all clear' function and lead to an increase in foraging and a decrease in vigilance behaviour in receivers, and warning calls, which decrease foraging and increase vigilance behaviour for the rest of the group (Rauber and Manser, 2017).

Contributions to sentinel behaviour reduce foraging opportunities. The costs of foregoing foraging are likely to increase under adverse environmental conditions, leading to stronger trade-offs between cooperative behaviours and individual survival. Average rainfall in our study area in the Southern Kalahari since 2009 has been 98 mm between December and January but due to the severe El Nino event in 2015/16 rainfall was less than 1 mm during the same time period and the weight and breeding success of resident animals was reduced ((Wiley and Ridley, 2016); unpublished data long-term database). To test whether and how drought conditions affected cooperative behaviours, we measured the contributions of

individuals to sentinel behaviour during a year of drought, three dry years of low rain conditions and three wet years of high rain conditions (Table 1). In particular, we investigated the effects of drought on the probability to act as a sentinel and the duration of guarding periods. We predicted that while meerkats should be adapted to dry years, drought conditions increase the costs of cooperative behaviours. As a consequence, we expected to find that animals reduce both the probability that individuals would go on sentinel guard and the duration of sentinel bouts in order to increase foraging time and thus individual survival. We expected this effect to be most pronounced in younger individuals and members of small groups, whose foraging success is relatively low (Clutton-Brock et al., 1999b; English et al., 2014). Furthermore, we expected drought to decrease the skew in guarding contribution within groups as single individuals might not be able to maintain higher sentinel frequencies compared to the rest of the group. In regards to vocal coordination, we investigated the consequences of drought on the responses of individuals to sentinel warning and calming calls, using a series of playback experiments. We predicted that under drought conditions foraging meerkats respond stronger to sentinel calming calls ('all-clear' function) and reduce their response to sentinel warning calls (pre-stages of alarm calls) to increase foraging efficiency in comparison to non-drought conditions (Rauber and Manser, 2017).

METHODS

Study site and species

Data were collected at the Kalahari Meerkat Project (KMP) located at the Kuruman River Reserve in the southern Kalahari Desert, Northern Cape, South Africa (for more information about habitat at the study site see (Clutton-Brock et al., 1999; Russell et al., 2002). The climate at the study site is characterised by two distinct seasons: a cold-dry season from May to September (mean monthly rainfall 5.5ml) and a hot-wet season from October to April

134 (mean monthly rainfall 45.7ml) (Clutton-Brock et al., 1999; Russell et al., 2002). As part of
135 the KMP's long-term data collection, all group members were uniquely dye marked to allow
136 individual recognition, and one or two individuals of each group were fitted with radio-collars
137 to facilitate localisation of the group (Jordan et al., 2007). All groups were habituated to close
138 human observations and to the playback equipment, allowing us to perform recordings and
139 playbacks within a distance of 0.5 m to the test subjects.

140

141 *Analysis of long-term data*

142 Individual sentinel events and their durations were collected between December and January
143 from 2009 to 2016 by volunteers of the Kalahari Meerkat Project as part of the daily long-
144 term data collection. We assigned each period of these seven years to one of three
145 environmental conditions – wet, dry and drought- based on the amount of rainfall measured
146 directly at the study site during the middle of the wet season, which includes the months
147 December and January. To account for any carry-over effects from previous rainfalls, we also
148 added the amount of rainfall during the three months before the analysed periods, i.e.
149 September to November. This resulted in the following categorisation: 2009/2010, 2010/2011
150 and 2011/2012 represented wet years, 2012/2013, 2013/2014 and 2014/2015 were dry years,
151 and 2015/2016 was a drought year with almost no rain between December and January (Table
152 1). A sentinel event always consisted of an individual climbing on an elevated position of at
153 least 10cm above ground and actively scanning the environment (Clutton-Brock et al.,
154 1999b). To investigate whether the different environmental conditions affected the probability
155 of individuals to go on guard we included every individual (total n=750; n=266 adults, n=504
156 yearlings, n=370 subadults, n=193 juveniles, due to the multi-year data structure some
157 individuals appear in several age categories) from every group (n=26) in the analysis and
158 checked whether each of these individuals acted as sentinel or not for each observation day
159 (n=28'773 observations). This resulted in a daily yes/no response variable for every group

member present on the day of data collection. Following this, we compared observed daily sentinel durations by calculating the total time individuals were on sentinel guard during the 3.2±0.02 hours of observations per day (including morning and evening sessions) resulting in a total of 3969 sentinel events of 480 different individuals (n=179 adults, 312 yearlings, 180 subadults, 21 juveniles, due to the multi year data structure some individuals appear in several age categories). All individuals' age, sex, dominance status, group size, and whether and how many pups were in the group were documented. We investigated the effect of any interaction between environmental condition and age, sex, dominance status, group size, presence of pups and number of pups on the observed time (min) individuals spent on sentinel duty per day.

Sound recordings

Sound recordings for the playbacks of the different sentinel call types were collected in May 2014 prior to the start of the first playback experiments. Calls from naturally occurring sentinel events were recorded using a Sennheiser directional microphone (ME66/K6) connected to a Marantz PMD-670 solid-state recorder (Marantz Japan Inc.; sampling frequency 44.2 kHz, 16 bits accuracy). A Rainhardt microphone windshield (W200) was permanently attached to the microphone to ensure high quality recordings in the meerkats' natural environment. The microphone was fixed to a telescopic pole in order to maintain a recording distance of less than 0.5 meters and a high signal-to-background ratio.

Playback experiments

In order to compare behavioural responses to sentinel vocalisations during a non-drought and a drought condition we repeated the same series of playbacks we had done for previous work (Rauber and Manser, 2017) in the non-drought period from June to August 2014 in the drought period of 2015/2016 from January to the 8th of March 2016. The rainfall measurements for these two periods differed substantially in regards to the amount of rain in

187 the 3 months period before and the 3 months period of the playback experiments, with the
188 non-drought period having received 112ml and the drought period 15.2ml over the total of 6
189 months. When testing the probability to act as sentinel, this was significantly higher during
190 the non-drought period compared to the drought period (GLMM; $\beta \pm se = 1.32 \pm 0.39$, $z = 3.41$, $p < 0.001$), indicating that, besides any other potential seasonal differences,
192 environmental conditions were less constraining for meerkats during the non-drought period.
193 We conducted playback experiments in a total of 12 groups with group size of three to 24
194 individuals. Following the same protocol as previous work on the behavioural response to
195 sentinel vocalisations (Rauber and Manser, 2017), we selected single calls with a high signal-
196 to-noise ratio using Cool Edit Pro (Syntrillium Software Corporation) to compose playback
197 files consisting of sentinel calls and close calls (control) from the same individual. Close calls
198 are soft, close range contact calls that are frequently emitted during foraging and used for
199 group coordination (Fichtel and Manser, 2010; Gall and Manser, 2017).
200 Sentinel calls of recordings from at least six different and independent recording events from
201 the same individual (n=8) were used for each playback file. The calls from at least three
202 different individuals were played back to each group, using a Marantz PMD-670 solid-state
203 recorder, connected to a portable speaker (iHome IHM79SC). The amplitude was assessed
204 according to how the calls occur under similar natural weather and wind conditions. The call
205 rate of the specific sentinel calls and close calls was kept the same as observed in natural
206 recordings (close calls: 8.25 ± 2.28 calls/min; single note calls: 3.79 ± 0.43 calls/min; double
207 note calls: 3.19 ± 0.37 calls/min) with background noise between each call (Rauber and
208 Manser, 2017). For the sentinel warning calls context we always played a total of four calls,
209 two “di-drrr” and two “wheek” calls in alternating order and with at least one minute of
210 background noise in between, which also lies in the range of natural recordings (di-drr: 0.34 ±
211 0.12 calls/min; wheek calls: 0.39 ± 0.09 calls/min (Rauber and Manser, 2017)). Playback
212 experiments were only conducted when no predator had been seen for at least 15 minutes and
213 only if the majority of the group was foraging undisturbed for at least five minutes. If any of
214 the conditions, including the absence of predators, were violated after the playback had been

started, the playback was paused and resumed only after the majority of the group was back to normal foraging behaviour for a minimum of five minutes or the sentinel finished its guarding session. We played back a series of six five-minutes sound files to an adult foraging meerkat, resulting in playbacks of a length of 30 minutes each. The full playback consisted of five minutes of the two different sentinel call types (i.e. calming and warning calls), five minutes of close calls (cc) in the beginning, between the two types of sentinel calls and afterwards and also five minutes of background noise (bkg) either at the very beginning or the end (e.g. cc-calming-cc-warning-cc-bkg). During the playbacks each behaviour of the test subjects was recorded as a focal follow using the program Cybertracker (Cybertracker Conservation 2013 version 3.376) on a handheld tablet (Acer IconiaOne 7 B1–750). Four adult individuals (>12 months, the dominant pair and one subordinate of each sex) of eight groups were tested to playbacks, resulting in a sample size of 32 playbacks for each year. To keep the playback procedure the same as in 2014, when we were also interested in the potential difference between calls from the same versus from another group, half of the playbacks were from individuals from the same group and the other half from individuals from another group.

Analysis of behavioural focals

Behavioural responses to sentinel calls are of short duration and are only obvious within the first 30 seconds after the playback of a call (Rauber and Manser, 2017). Therefore, to analyse the response of the test subjects we calculated the proportion of time the meerkats spent foraging and being vigilant during the first 30 seconds after four randomly (sample function of the R base package) chosen calls of each of the different playback contexts (close calls, calming sentinel calls, warning sentinel calls). As each playback file consisted of three identical copies of five-minute tracks of close calls the proportions of time spent for each behaviour was averaged for the analysis (here after called average cc). For the background noise context we chose four random time points and analysed the behaviour in the following 30 seconds. As foraging behaviour we grouped foraging (digging in a hole for prey),

242 scrabbling (head down while scratching at multiple small holes or surface), processing
243 (processing food items in sand, or chewing off tail of scorpions, etc.) and eating. Regarding
244 the alert-related behaviours, we focused on two types of vigilance behaviour: quadrupedal
245 (head up while scanning the sky and the surroundings on all four legs) and bipedal (scanning
246 of sky and surroundings standing on the hind legs with upright body position).
247
248 *Statistical analysis*

249 All analyses in this study were done using R version 3.2.0 (R Development Core Team 2016).
250 To determine the relationship between sentinel behaviour and the different parameters we
251 conducted linear mixed effects models (LMM) and generalized linear mixed effects models
252 (GLMM), depending on whether the data met the assumptions of normality and homogeneity
253 of variance (Bates D., 2014). To determine the fit of linear mixed models we examined the
254 model diagnostic plots and response variables were transformed where assumptions of the
255 models were not met (Crawley, 2012) . Post-hoc multiple comparison tests with manually set
256 contrasts were done whenever the predictor variable consisted of more than two categories to
257 compare the different categories not specified by the intercept (Hothorn T., 2008).
258 To analyse the effect of environmental conditions on an individual's observed daily
259 probability to go on guard, we fitted a generalized linear mixed effects model with guarding
260 (0/1) as response variable, thus, using binomial distribution. Because there was no significant
261 difference of guarding between wet and dry years while they were both significantly different
262 from the drought year we pooled those together as 'non-drought years' to facilitate model
263 convergence. Age class, sex, dominance status, group size, presence of pups and number of
264 pups were each tested as interaction with drought as fixed effects and Individual ID nested in
265 Group ID and Observation Date were added as random effects.
266 To investigate the effect of environmental conditions on sentinel duration we fitted a LMM
267 with individual sentinel guarding time per observation day as response variable and again age
268 class, sex, dominance status, group size and presence of pups were each tested separately as

interaction with drought as fixed effects. Individual ID nested in Group ID were added as random effects. To determine whether sentinel duties were more evenly distributed within the group during the drought compared to wet and dry years we calculated the proportion of different sentinel individuals as the number of all individuals acting as sentinel per observation day divided by the total group size (not including pups which don't contribute to sentinel behaviour (Hollen et al., 2008)). We then used the log-transformed proportion of sentinels as response variable in a LMM with environmental conditions, group size and the interaction between drought and group size as fixed effects and Group ID as random factor. Since there was again no difference between dry and wet years while both being significantly different from drought, we pooled these two conditions together as non-drought period to improve model convergence. Lastly, to analyse the effect of environmental conditions on the response to sentinel calls (playback experiments) and the two different control conditions (close calls and background noise), we conducted generalized mixed models with the proportion of the behaviour of interest (number of seconds out of the total 30 seconds after a call) as response variable using the cbind function and family binomial (Crawley, 2012). Individual ID was nested in Group ID as random factors. The three behaviours of interest were foraging, quadrupedal vigilance and bipedal vigilance. Whenever the explanatory variable consisted of more than two categories multiple comparison test with manually set contrasts (glht function of multcomp package) were used to compare the different categories not specified by the intercept, or to compare specific contrasts (Hothorn T., 2008). The p values were generated using adjusted p values using Bonferroni correction (Hothorn T., 2008).

Ethical note

All the experiments and recordings conducted within the course of this study fall under the permission of the ethical committee of Pretoria University and the Northern Cape

295 Conservation Service, South Africa (Permit number: EC031-13) and were carried out
296 adhering to the approved guidelines in this permit.

297

298 RESULTS

299

300 *Effect of environmental conditions on probability that individuals act as sentinel*

301 While there was no difference in the probability that individuals acted as sentinels during wet
302 and dry years ($\beta = 0.13 \pm 0.23$, $z = 0.55$, $p = 0.583$), meerkats went on sentinel guard
303 significantly less during the drought condition compared to the dry ($\beta = -1.01 \pm 0.32$, $z = -3.18$,
304 $p = 0.001$) and wet conditions ($\beta = -0.89 \pm 0.33$, $z = -2.67$, $p = 0.007$). Therefore, wet and dry
305 conditions were pooled together as 'non-drought' conditions and then compared to the
306 drought condition. During the drought condition, we found that, juveniles and subadults
307 reduced the frequency of them acting as sentinel significantly more than adults (Table 2;
308 Figure 1a). The same decrease was observed with yearlings, however, less strong. This
309 reduction in sentinel frequency was stronger in smaller groups and in groups where pups were
310 present (Table 2; Figure 1a,b). There was no interaction between environmental conditions
311 and either dominance status or sex on the likelihood to show sentinel behaviour.

312

313 *Effect of environmental conditions on sentinel duration*

314 The dry condition had a negative effect on the duration to stay on sentinel guard compared to
315 wet conditions ($\beta = -0.11 \pm 0.03$, $t = -3.5$, $p < 0.001$; Figure 2). The drought condition was not
316 significantly different from dry ($\beta = 0.04 \pm 0.05$, $t = 0.84$, $p = 0.403$; Figure 2) or wet ($\beta = -$
317 0.06 ± 0.05, $t = -1.03$, $p = 0.304$; Figure 2) conditions. None of the tested variables including
318 age class, sex, dominance status, group size and presence of pups showed a significant
319 interaction with the three environmental conditions (wet, dry and drought).

320

Effect of environmental conditions on distribution of sentinel duties among group members

The proportion of individuals contributing to sentinel behaviour within a group was significantly lower during the drought compared to the dry (β = -0.06±0.02, t = -3.04, p = 0.003) and the wet (β = -0.05±0.02, t = -2.16, p = 0.031) conditions. Dry and wet conditions did not differ (β = 0.01±0.01, t = 1.16, p = 0.247), thus were pooled together to non-drought conditions. There was an interaction between environmental conditions and group size such that, for small groups during drought conditions, the proportion of individuals contributing to sentinel behaviour was the same or slightly higher than during non-drought conditions, while the opposite was true for larger groups. They showed significantly lower proportions of sentinels during the drought (Table 3; Figure 3). Follow up analyses excluding very small groups of less than six individuals, as well as very large groups of more than 22 individuals, confirmed the robustness of this result.

Effects of environmental conditions on response to sentinel calls

Foraging meerkats responded differently to the four tested playback conditions during the drought in comparison to the non-drought period. The playback of sentinel calming calls elicited less bipedal vigilance in the drought compared to the non-drought period (Table 4; Figure 4c). Close calls (average cc), on the other hand, led to more foraging behaviour during the drought (Table 4; Figure 4a), while background noise tended ($p<0.1$) to elicit less foraging behaviour (Table 4, Figure 4a) and more quadrupedal vigilance behaviour (Table 4; Figure 4b) during the drought period. We did not, however, find any evidence, that warning sentinel calls were more likely to be ignored during the drought period (Table 4; Figure 4c).

DISCUSSION

Our results show the frequency of cooperative behaviours in meerkats to be significantly reduced during naturally occurring, extreme environmental conditions with

limited food availability, supporting previous work on food dependency of cooperative behaviours. While the probability of cooperative sentinel behaviour was the same during commonly occurring dry and wet years, in the extreme drought year with almost no rain, a shift in the investment from cooperative behaviours to foraging behaviour with immediate individual benefits was observed, and vocal group coordination was also affected. During the drought year, individual meerkats reduced the frequency with which they contributed to sentinel behaviour. These reductions were largest in young individuals of less than two years, members of smaller groups, and in groups with pups. Compared to smaller groups, in larger groups the contribution to sentinel behaviour was less evenly distributed among group members during the drought compared to the non-drought (dry and wet years taken together) periods. Meerkats also responded more strongly to calming sentinel calls and contact calls, showing more foraging and less vigilance behaviour in the drought year than in a year with wet conditions. Background noise, however, led to less foraging and more vigilance behaviour in the drought year.

In accordance with our predictions, we found that within groups, especially young individuals, i.e. juveniles and subadults, were less likely to act as sentinel during the drought. Yearlings (1-2 years old) also showed less sentinel behaviour during the drought compared to adults, however, the effect was less strong than in the younger age class. Furthermore, we found that group size and composition significantly affected the probability to act as sentinel when comparing the drought year with the dry and wet years. Members of small groups and groups with pups reduced the sentinel frequency during the drought more than members of larger groups and groups without dependent offspring. The effect of group size is likely explained by the higher individual contribution to sentinel behaviour in smaller groups (Clutton-Brock et al., 1999b). The found effect of presence of pups suggests that having dependent offspring (pups) comes with additional costs of helping behaviours such as allolactation, pup feeding and protection of pups (Clutton-Brock and Manser, 2016). As the survival of young is critically dependent on provisioning from adults, it is not surprising that these behaviours are prioritized over sentinel behaviour as a response to limited resources.

Duration of sentinel behaviour per guarding event was longest during wet years. A likely explanation is that during these conditions vegetation is usually much taller and denser compared to dry years and the drought year and meerkats need to stay on sentinel guard longer in order to scan the area for the presence of predators, in particular terrestrial predators. In addition, there is more food available in the wet season leading to individuals being faster satiated and thus able to afford to be on sentinel guard for longer periods of time. Against our predictions, we did not find a difference in sentinel duration between the dry years and the drought year. The reduction in sentinel duration in dry years may be due to the fact that compared to the drought year meerkats still keep up the same frequency of sentinel behaviour during dry years as during wet years when food is plentiful. Therefore, when conditions get harder there seems to be a trade-off between frequency of cooperative behaviours and duration. During dry years it seems that mainly duration was reduced while during the drought year it was mainly the frequency that decreased with which individuals maintain cooperative behaviours. Further research is needed to explore this relationship in other cooperative behaviours, in particular using more drought years.

In terms of how sentinel behaviour is distributed among group members, we provide evidence that larger groups showed a bigger decrease in the number of different individuals going on sentinel guard per day in the drought, while the proportion of individuals acting as sentinel of smaller groups stayed the same as in non-drought years. Together with the effect of group size on the probability to act as sentinel, this suggests that in smaller groups, the same number of animals go on shorter sentinel bouts, while in larger groups fewer animals act as sentinels in the drought, but those can afford to keep the total time the group has a sentinel similar to non-drought years. Thus, larger groups were able to maintain cooperative behaviours, while cooperative behaviours in smaller groups were significantly reduced in the drought year. This is in line with previous work that shows the benefits of living in larger groups due to lower individual contribution to cooperative behaviours (Clutton-Brock et al., 1999b).

404 Not only investment into sentinel behaviour changed depending on environmental
405 conditions, but also the vocal coordination of foraging meerkats. Test subjects responded
406 more strongly to playbacks of sentinel calming calls, which act as 'all-clear' signal, resulting
407 in less vigilance and more foraging behaviour in the drought period in comparison to the non-
408 drought period. A likely explanation is that during demanding conditions individuals rely
409 more on 'all-clear' signals in order to maximize foraging. We did not, however, find any
410 evidence that meerkats were more likely to ignore sentinel warning calls in the drought period
411 compared to the non-drought period. This is in line with work on alarm calls, where the costs
412 of not responding to calls related to predators have been suggested to be too high to ignore
413 (Schibler and Manser, 2007). The fact that meerkats were more vigilant during the drought
414 when they heard background noise may indicate, that as a consequence of the decrease in
415 cooperative vigilance behaviour, individuals experience higher levels of uncertainty in
416 perceived predation risk and thus invest more time into personal vigilance behaviours.
417 Additionally, hearing no calls from other group members might increase the perceived risk of
418 loosing the group (Gall and Manser, 2017), due to meerkats being more spread out when food
419 is spatially and temporally more scattered (Rymer et al., 2016). This is supported by findings
420 that during drought conditions foraging meerkat groups split more often compared to dry
421 conditions (Gall, 2017) and can also explain our result that meerkats were less vigilant when
422 they heard contact calls during the drought, indicating close proximity to other group
423 members (Gall and Manser, 2017). However, other differences in seasonal related factors, e.g.
424 spatial cohesion or foraging time, between the two playback periods, besides the amount of
425 rain and sentinel frequency, can not be excluded to have impacted the behavioural response of
426 foraging meerkats to sentinel calls. Further playbacks are needed to confirm the importance of
427 specific environmental factors on a species' communication system.
428 In conclusion, our results suggest that naturally occurring, extreme environmental
429 conditions, such as droughts, decrease the contribution to cooperative behaviours, as shown
430 on the sentinel behaviour in meerkats. Furthermore, these reductions in frequency and to a
431 lesser extent duration of cooperative vigilance behaviour were associated with changes in the

vocal coordination of foraging meerkats. Although meerkats, and cooperative breeders in general, are adapted to arid, unpredictable environments (for example (Cockburn and Russell, 2011; Schneider and Kappeler, 2014), extreme environmental conditions that reduce food availability affect the investment of individuals in cooperative activities and the vocal coordination of cooperative behaviours. Therefore, we argue that there is likely an ecological threshold beyond which some aspects of cooperation including cooperative vigilance behaviour and provisioning of young (Wiley and Ridley, 2016) seem to collapse. Our study offers new insights about how extreme environmental conditions influence the occurrence of cooperative behaviours and the consequences for group coordination in cooperative breeders.

AUTHORS' CONTRIBUTIONS

RR and MBM were involved in planning the study. RR conducted the experiments and statistical analyses. RR, MBM and THCB equally contributed to the writing of the manuscript. THCB and MM organised the long-term data collection at the KMP on cooperative behaviour, weights and life history data.

COMPETING INTERESTS

We declare we have no competing interests.

FUNDING

RR, MBM and research expenses were funded by the University of Zurich, THCB was funded by the University of Cambridge. The long-term field site KMP was financed by University of Cambridge and Zurich, and the MAVA foundation. This paper has relied on records of individual identities and/or life histories maintained by the KMP, which has been supported financially by the European Research Council (Grant No 294494 to T.H. Clutton-Brock since 1/7/2012) and the University of Zurich, as well as logistically by the Mammal Research Institute of the University of Pretoria.

ACKNOWLEDGEMENTS

We thank the Kalahari Research Trust and the Northern Cape Conservation Authority for research permission (FAUNA 1020/2016). We also thank Dave Gaynor for organising the field site as well as the managers and volunteers of the Kalahari Meerkat Project (KMP) for organising and helping to collect the data about sentinel behaviour and life history of the meerkats. Furthermore, we thank Matthew Petelle, Gabriella Gall and Sabrina Engesser and two anonymous reviewers for comments on the manuscript.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by (Rauber et al., 2019).

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580 TABLES

581

582 **Table 1.** Environmental conditions based on rainfall measured at study site.

Year	Rainfall (ml) December-January (study period)	Rainfall (ml) September-November	Total amount of rain (ml) September - January	Environmental Condition (EC)
2009/2010	178.0	NA	178.0*	Wet
2010/2011	195.2	28.6	223.8	Wet
2011/2012	116.4	1.0	117.4	Wet

2012/2013	16.6	15.4	32.0	Dry
2013/2014	57.4	5.8	63.2	Dry
2014/2015	24.6	16.4	41.0	Dry
2015/2016	0.6	11.6	12.2	Drought

583 *minimum estimate due to lack of rain data at study site before December 2009
584

585 **Table 2.** GLMM model output investigating the interactions between environmental
586 condition (EC) and sex, age class, dominance status, group size, presence and number of pups
587 on observed daily sentinel probability (Number of obs=28773, groups: Code:Group=901;
588 WatchDate= 210; Group=35).

Fixed Effect	Effect±SE	Df	X^2	P
(Intercept)	-2.54±0.26			
Environmental condition (EC)	**-1.92**±0.52	**1**	**54.20**	**<0.001**
AgeCategoryJuvAndSub	**-0.79**±0.10			**<0.001**
AgeCategoryYearling	**0.44**±0.08			**<0.001**
SexM	**0.48**±0.11			**<0.001**
DomStatusSub	0.11±0.12			0.329
GroupSize	**-1.49±0.13**			**<0.001**
PresencePups	**0.59±0.05**			**<0.001**
EC:AgeClass		**3**	**22.27**	**<0.001**
EC:JuvAndSub	**-1.00±0.39**			**0.012**
EC:Yearling	**-0.59±0.27**			**0.026**
EC:Groupsize	**1.68±0.53**	**1**		**0.002**
EC:PresencePups	**-0.83±0.27**	**1**	**2.71**	**0.002**
Random effects	**Var**	**sd**		
Code:Group	**1.61**	**1.27**		
WatchDate	**1.91**	**1.38**		

589 Significant variables are shown in bold.

590 **Table 3.** Main effects and interaction of environmental condition (EC) and group size on the
591 proportion of different sentinels within a group (as determined by a linear mixed model;
592 Number of obs= 883, groups: Watch Date= 175; Group=25).

Fixed Effect	Estimate± SE	Df	X^2	P
(Intercept)	-0.99±0.07			
Environmental Condition (EC)	0.20±0.21	1	35.65	0.335
Group size	-0.05±0.01	1	215.25	**<0.001**
EC:Group size	-0.04±0.01	1	0.99	**0.003**
Random effects	**Var**	**sd**		
Group	**0.04**	**0.21**		
WatchDate	**0.01**	**0.09**		

593 Significant variables are shown in bold.

Table 4. GLMM model output and post-hoc multiple comparison test to compare foraging, quadrupedal vigilance and bipedal vigilance during the different playback conditions between drought and non-drought year (Numer of obs=946, number of playbacks=60, Code:Group=56, Group=12).

Behaviour	Condition	Estimate± SE	z-value	*P*
Foraging	(Intercept)	2.88±0.30		
	Close calls	**0.84±0.41**	**2.04**	**0.04**
	Background	-0.70± 0.41	-1.73	0.08
	Calming	0.49±0.43	1.12	0.26
	Warning	0.04±0.39	0.09	0.93
Quadrupedal	(Intercept)	-4.13±0.28		
Vigilance	Close calls	-0.22±0.33	-1.42	0.15
	Background	**0.71±0.32**	**2.45**	**0.01**
	Calming	-0.08±0.35	-0.29	0.77
	Warning	-0.11±0.31	-0.65	0.52
Bipedal	(Intercept)	-3.11±0.27		
Vigilance	Close calls	-0.62±0.37	-0.67	0.09
	Background	-0.42±0.37	-1.12	0.26
	Calming	**-1.02±0.38**	**2.67**	**0.007**
	Warning	-0.17±0.36	0.48	0.63

Significant variables are shown in bold.

FIGURES

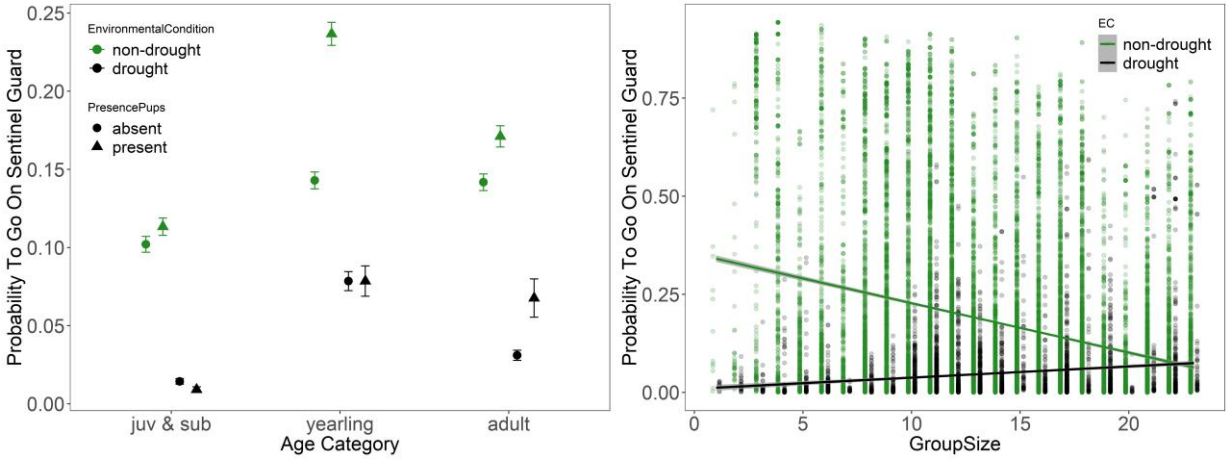

Figure 1. Model estimates of the daily probability to go on sentinel guard during drought (black) and non-drought (green; wet and dry conditions pooled together as they were statistically not different) for a) the different age classes and whether there were pups present in the group or not and b) different group sizes. Shown are estimates for subordinates only, which did not differ from dominant individuals.

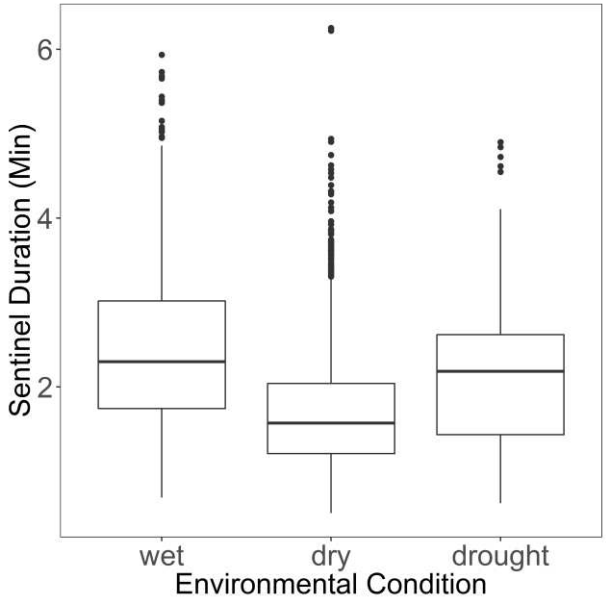

Figure 2. Boxplots of average predicted duration of a single sentinel event (in min) during each of the three environmental conditions (wet, dry, drought). The bold horizontal line represents the median while the box shows the interquartile range between the 25% and 75% percent quartiles. Whisker show data range of 1.5 times the interquartile range from the 25% and the 75% quartiles.

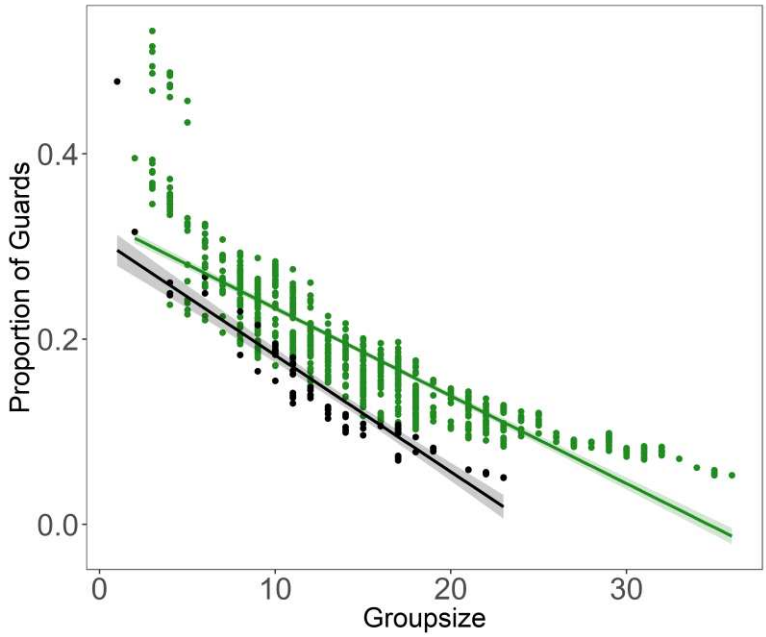

Figure 3. Relationship between predicted daily proportions of individuals in a group that acted as sentinels during drought and non-drought periods (wet and dry conditions pooled together as they were statistically not different).

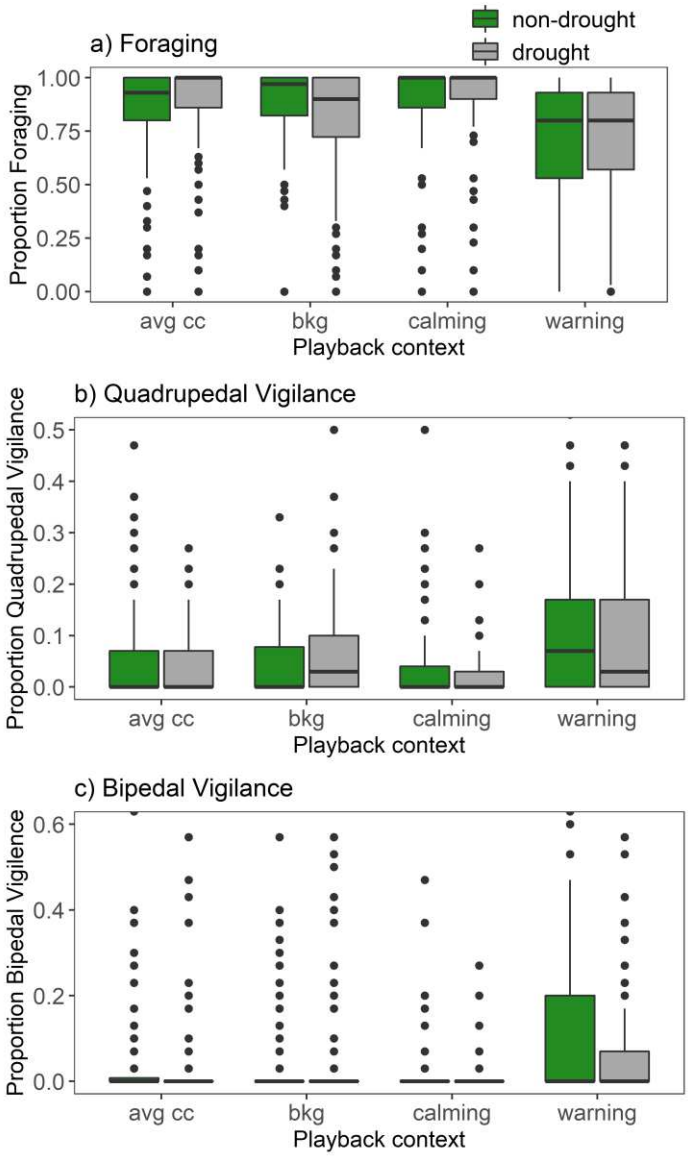

Figure 4. Comparison of (a) foraging, (b) quadrupedal vigilance and (c) bipedal vigilance behaviour given in response to the four different playback conditions (close calls (= average cc), background noise (bkg), calming sentinel calls, warning sentinel calls) between drought and non-drought period.